

THE MAYACACEAE
IN THE SOUTHEASTERN UNITED STATES¹

JOHN W. THIERET

MAYACACEAE Kunth, Abh. Akad. Wiss. Berlin Phys. 1840: 93. 1842,
"Mayaceae," nom. cons.
(BOGMOSS FAMILY)

A monotypic family of herbaceous aquatic monocotyledons distinguished by "mosslike" habit; perfect, hypogynous, regular (actinomorphic) flowers with 2 perianth whorls; 3 stamens; unilocular gynoecium with three parietal placentae; loculicidal capsular fruit; and seeds with starchy endosperm, a minute apical embryo, and a "stopper" or "embryostegium" formed from the inner integument of the ovule.

Characteristic anatomical features cited by Tomlinson include the lack of hairs except in the leaf axils; the presence of longitudinal air canals in root, stem, and leaf segmented by transverse diaphragms of stellate cells; the absence of mechanical tissues, the reduced stelar tissues being sheathed in both stem and root by an endodermis (thickened in the stem); and the absence of secretory elements.

The Mayacaceae are of somewhat uncertain taxonomic position. Even their familial status has been questioned (Grisebach included them in the Xyridaceae). They share various features with one or more of several families: Centrolepidaceae, Commelinaceae, Eriocaulaceae, Rapateaceae, Restionaceae, and Xyridaceae. A convincing argument for closest relationship with Commelinaceae is presented by Hamann (1961). Tomlinson concluded that "it is probable that *Mayaca* originated from the same stock that has produced Eriocaulaceae, Commelinaceae, and Xyridaceae."

1. *Mayaca* Aublet, Hist. Pl. Guiane Franç. 1: 42; 3: pl. 15. 1775.

Simple or branched "mosslike" aquatic herbs with copiously leafy stems.

¹ Prepared for a generic flora of the southeastern United States, a joint project of the Arnold Arboretum and the Gray Herbarium of Harvard University made possible through the support of the National Science Foundation (Grant BMS74-21469, principal investigator, Carroll E. Wood, Jr.). This treatment follows the format established in the first paper in the series (Jour. Arnold Arb. 39: 296-346, 1958). The area covered includes North and South Carolina, Georgia, Florida, Tennessee, Alabama, Mississippi, Arkansas, and Louisiana. References that I have not seen are marked with an asterisk.

I am indebted to Dr. Wood for his careful review of the manuscript and for other aid and to the staff of the Lloyd Library, Cincinnati, for help in bibliographic matters. The illustration was drawn by Karen S. Velmure, under the direction of Kenneth R. Robertson, from preserved material collected by J. D. Ray, C. E. Wood, Jr., C. E. Smith, Jr., and R. J. Eaton in Seminole County, Florida, and from a kodachrome taken by C. E. Smith, Jr. at the same time.

Transverse diaphragms in roots producing in dried specimens the appearance of cross-striations. Leaves alternate, spirally arranged, sessile, lanceolate or linear-lanceolate to filiform, 1-nerved, commonly notched at the apex. Inflorescence of solitary axillary flowers [or of terminal simple umbelliform clusters]. Flowers perfect, regular, hypogynous, with 2 perianth whorls, the pedicels short to long, each bracteate at its base, the bracts ("spathes" or "hypsophylls") broad, membranaceous, delicate, shorter than the leaves. Calyx persistent, of 3 distinct, ovate or ovate-lanceolate to lanceolate sepals. Corolla of 3 distinct, ovate to rotund, white to pink petals. Androecium of 3 distinct stamens, these opposite the sepals; filaments linear, slightly widened at the base; anthers basifix, 2(?) or 4-sporangiate, 2- [or 4-] loculate at anthesis, opening through an apical or subapical pore or slit [or through an apical tube or cup]; pollen 1-sulcate, tenui-exinous, elliptic to broadly ovate. Gynoecium syncarpous, 3-carpellate; ² stigma undivided [or 3-lobed]; style 1, elongate, linear, persistent; ovary unilocular, with 3 parietal placentae; ovules 6-30, orthotropous. Fruit a 3-valved, loculicidal capsule; seeds ovoid or globose, reticulate-scrobiculate, with an apical "stopper" or "embryostegium," the endosperm starchy, the embryo minute and apical. TYPE SPECIES: *M. fluviatilis* Aublet. ("Aboriginal American name," according to Fernald; perhaps related to the Mayaca or Mahica region of Brazil, according to Lourteig, 1952.) — BOGMOSS.

A genus of four species (Lourteig, 1952), three of these in tropical and warm-temperate America and one (*M. Baumii* Gürke) in southern Africa (Angola, Zaïre, Zambia). One or two (?) species are found in our area: *M. fluviatilis* Aublet (including *M. Aubletii* Michx.?) occurs on the Coastal Plain of the southeastern United States (North Carolina to Florida, west to eastern Texas ³), in the West Indies and Central America, and in South America, south to Bolivia, northeastern Argentina, and Uruguay. It grows submersed or floating in water or creeping on soil or moss mats at margins of ditches, streams, ponds, lakes, swamps, and bogs.

Lourteig, the most recent reviser of the genus, recognizes only 4 species, other workers as many as 10. Such differences in taxonomic opinion derive in part from the great phenotypic plasticity of the bogmosses in response to different environmental conditions.

Like many aquatic genera, *Mayaca* shows great variation between emersed and terrestrial forms. Submersed plants of *M. fluviatilis*, for ex-

² A specimen of *Mayaca* from Wayne Co., Georgia (W. H. Duncan 7861, GH) bears the statement "ovary usually 3 carpellate (occasionally 4 or 5 carpellate) with usually 3 (occasionally 4 or 5) parietal placentae." The occurrence of supernumerary flowers in *Mayaca* seems not to have been noted in literature.

³ Reports of *Mayaca* from Virginia, dating back to Pursh, are ascribed by Fernald to misidentification of *Lycopodium inundatum* var. *Bigelovii*. Gleason's report of *Mayaca* from Ohio, for which I have been unable to locate a supporting specimen, may be based on similar confusion. Ulbrich's incidental mention of Kentucky in the range of *M. Aubletii* may safely be ignored, as may Muenscher's report of Pennsylvania in the range of this species.

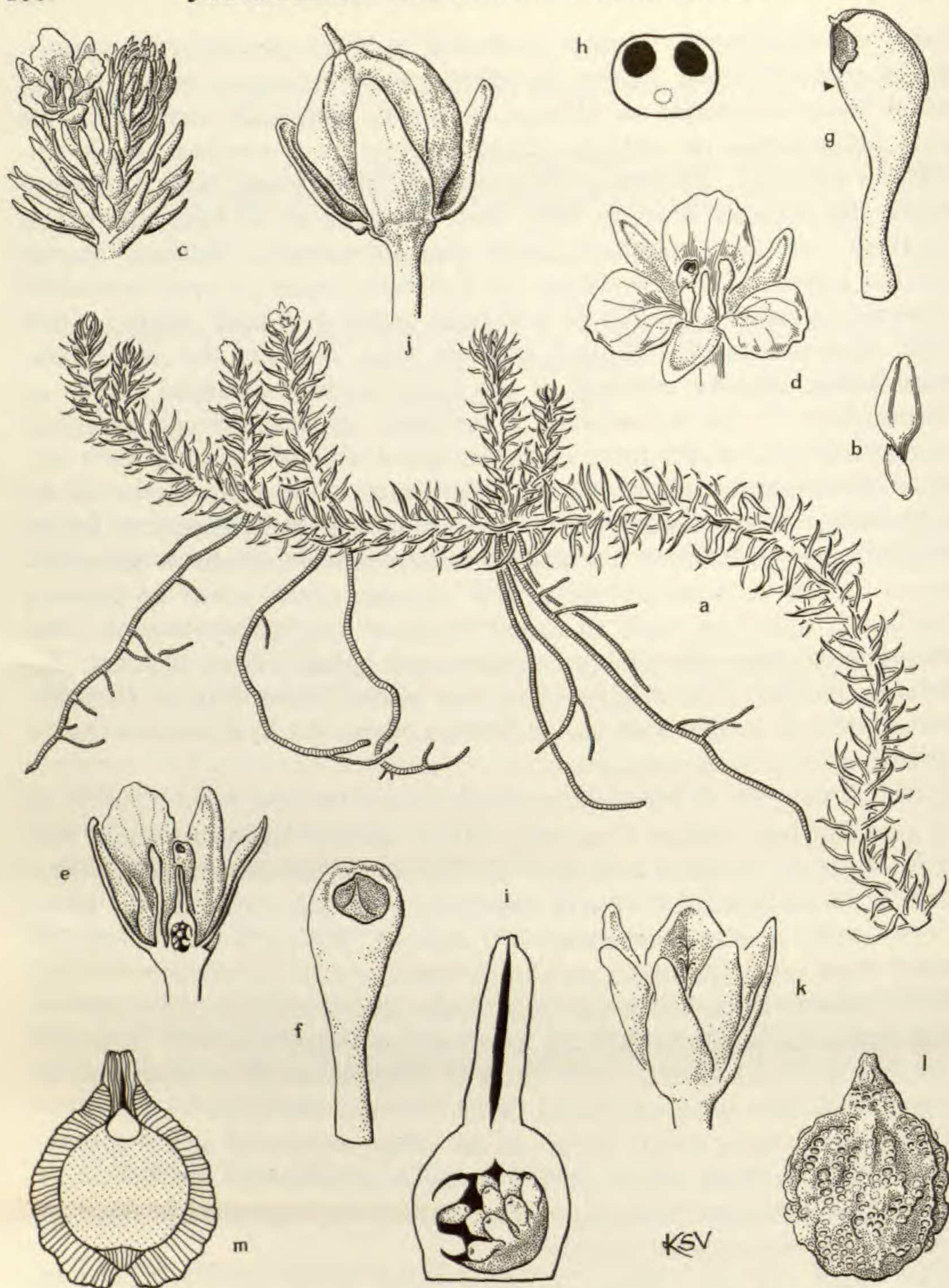


FIGURE 1. *Mayaca*. a-l, *M. fluvialis* (*M. Aubletii*): a, apical part of flowering plant — note cross-striated roots, $\times 1$; b, flower bud with subtending bract, $\times 3$; c, tip of stem with open flower, $\times 3$; d, flower, $\times 6$; e, flower in vertical section, $\times 6$; f, adaxial side of stamen — note dehiscence by apical pore, $\times 20$; g, lateral view of stamen, $\times 20$; h, cross section of stamen at level shown in "g," anther locules in black, vascular bundle in dots, $\times 25$; i, gynoecium in vertical section, one parietal placenta in section, one uncut — note orthotropous ovules and stylar canal, $\times 20$; j, nearly mature capsule, $\times 5$; k, dehisced capsule — note remains of placentae on valve, $\times 6$; l, seed, the micropyle up, $\times 25$; m, seed in vertical section, outer integument hatched horizontally, inner integument forming "stopper" hatched vertically, endosperm evenly stippled, embryo unshaded, $\times 25$.

ample, tend to have elongate stems with long-tapering, translucent, obviously spirally arranged leaves, while emersed plants generally have short stems with shorter, thicker, very closely imbricated leaves. Submersed forms have a thicker endodermis and a greater amount of aerenchyma than do emersed forms. *Mayaca* in the southeastern United States should be studied under controlled conditions to determine whether *M. fluviatilis* is the only representative of the genus there, as Lourteig concluded, or whether *M. Aubletii* is distinct, as claimed by some. The two taxa have been supposed to be distinguishable on the basis of weak, trailing, often submerged stems usually more than 40 cm. long in *M. fluviatilis* versus tufted or matted emersed stems only 2–20 cm. long in *M. Aubletii*; leaves 4–20 mm. long vs. 3–5 mm. long; pedicels shorter than the leaves vs. longer than the leaves; and capsules oblong-ellipsoid, nearly twice as long as broad, vs. subglobose or ovoid, nearly as broad as long. At least some of these characteristics are known to be environmentally influenced.

Of basic taxonomic value in *Mayaca* is the variation in the mode of dehiscence of the anthers, which open through an apical or subapical pore or slit (*M. fluviatilis*) or through an apical tube (*M. longipes*, *M. Sellowiana*) or cup (*M. Baumii*). A detailed developmental study of the stamens of *M. fluviatilis* is needed to determine whether the anthers are indeed 2-sporangiate and thus different from the usual 4-sporangiate condition in *Mayaca*, a claim made by Horn af Rantzien but denied by Lourteig (1952). Kenneth R. Robertson, in a series of freehand sections made for FIGURE 1, found "no evidence of four locules" (C. E. Wood, *in litt.*). The Mayacaceae are unknown cytologically and embryologically.

The broadly ovate bract subtending each pedicel splits longitudinally into halves when it is still relatively young, often even before the pedicel elongates fully. Literature reports of the pedicels of *Mayaca* being *bibracteate* at the base derive from misinterpretation.

Pollination mechanisms in *Mayaca* have been little investigated. Uphof (1933) noted no insect visitors to the flowers of *M. fluviatilis* in Florida and suggested the possibility of anemophily. He reported fruit development both from aerial and from submersed cleistogamous flowers.

The seeds of *Mayaca* are characterized by an "embryostegium" (or "stopper") at their micropylar end (FIGURE 1, k–l). This structure, just distal to the embryo, is apparently developed from the inner integument, the growth of which exceeds that of the outer. The cells of the "stopper" are thinner walled than those of the testa, which is formed from the outer integument. Hamann (1961) suggests that disintegration of the "stopper" may provide a canal for emergence of the seedling.

The seeds are dispersed, so far as is known, by water. In one experiment (Ludwig), seeds of *M. fluviatilis* germinated promptly in water after six weeks of drying, but seeds kept submerged had not begun to germinate even after twelve weeks.

Mayaca fluviatilis and perhaps other species of the genus fare poorly in competition with other plants.

Mayaca may rarely be used as an aquarium plant. Other than this, the genus has no economic importance.

REFERENCES:

- ARBER, A. Leaves of the Farinosae. *Bot. Gaz.* **74**: 80–94. 3 *pls.* 1922. [Mayacaceae, 82, *pl.* 3, fig. 27, *A–B*; gross anatomy.]
- AUBLET, F. *Histoire des plantes de la Guiane Françoise*. 4 vols. 392 *pls.* London & Paris. 1775. [*M. fluviatilis*, 1: 42–44; 3: *pl.* 15.]
- BAILLON, H. Mayacacées. *Hist. Pl.* **13**: 230, 231. 1895.
- BATE-SMITH, E. C. The phenolic constituents of plants and their taxonomic significance. II. Monocotyledons. *Jour. Linn. Soc. Bot.* **60**: 325–356. 1968. [*M. Sellowiana*, 334; chromatography of leaf hydrolysates.]
- BENTHAM, G., & J. D. HOOKER. Mayaceae. *Gen. Pl.* **3**: 843. 1883.
- BOUBIER, A. M. Remarques sur l'anatomie systématique des Rapateacées et des familles voisines. *Bull. Herb. Boiss.* **3**: 115–120. 1895. [Mayacaceae, 119, 120.]
- BOUTIQUE, R. Mayacaceae. In: *Flore du Congo, du Rwanda et du Burundi*. Jard. Bot. Natl. Belg. 4 pp. 1971. [*M. Baumii* Gürke.]
- . Mayacaceae. *Distributiones plantarum africanarum*, Jard. Bot. Natl. Belg. **3**: 90. 31 Dec. 1971. [*M. Baumii*.]
- BRUGGEN, H. W. E. VAN. *Mayaca* species. *Aquarium Den Haag* **28(7)**: 153, 154. 1958.
- CASTELLANOS, A. Mayacaceae. In: H. R. DESCOLE, *Gen. Sp. Pl. Argentinarum* **3**: 21–37. *pls.* 3–5. 1945.
- . Algunas especies de plantas interesantes para la flora Uruguaya. *Lilloa* **20**: 237–249. 1949. [*M. Vandellii*, 240, 241, new to flora of Uruguay.]
- CORRELL, D. S., & H. B. CORRELL. Aquatic and wetland plants of southwestern United States. xvi + 1777 pp. *frontisp.* Water Pollution Control Res. Ser., Environ. Protect. Agency. [Washington, D. C.] 1972. [Mayacaceae, 578, *fig.* 297.]
- & M. C. JOHNSTON. Manual of the vascular plants of Texas. xv + 1881 pp. *frontisp.* 1 *map*. Renner, Texas. 1970. [Mayacaceae, 347, 348.]
- ENDLICHER, S. *Genera plantarum*. 2 vols. Vindobonae. 1836–1840. [*Mayaca*, 1: 124.]
- ENGLER, A. Mayacaceae. *Nat. Pflanzenfam.* II. **4**: 16–18. 1888.
- . Die Pflanzenwelt Afrikas. II. Charakterpflanzen Afrikas. Vol. 9 in A. ENGLER & O. DRUDE, *Die Vegetation der Erde*. 460 pp. Leipzig. 1908. [Mayacaceae, 259, 260, *fig.* 175.]
- ERDTMAN, G. Pollen morphology and plant taxonomy. *Angiosperms*. xii + 539 pp. Waltham, Mass. 1952. [Mayacaceae, 266.]
- FERNALD, M. L. Additions to and subtractions from the flora of Virginia. *Rhodora* **49**: 85–115, 121–142, 145–159, 175–194. 1947. ["Is *Mayaca* in the 'Manual Range'?", 130; no.]
- GANDOGER, M. *Sertum plantarum novarum*. Pars secunda. *Bull. Soc. Bot. France* **66**: 286–307. 1919. [*M. longipes* & *M. caroliniana*, spp. nov., 293; types from southeastern United States.]
- GLEASON, H. A. Notes from the Ohio State Herbarium. IV. *Ohio Nat.* **6**: 397, 398. 1905. [*M. Aubletii* reported erroneously from Ohio, 398.]
- GRISEBACH, A. *Catalogus plantarum Cubensium*. iv + 301 pp. Lipsiae. 1866. [*Mayaca*, 224, included in Xyridaceae.]
- GÜRKE, M. Eine neue *Mayaca*-Art aus Afrika. *Bot. Jahrb.* **31**(Beibl. 69): 1, 2. 1901. [*M. Baumii* described from Benguela.]
- HAMANN, U. Merkmalsbestand und Verwandtschaftsbeziehungen der Farinosae.

- Willdenowia 2: 639–768. 1961. [Mayacaceae, 719, 720, *passim*; discussion of relationships of family.]
- . Weiteres über Merkmalsbestand und Verwandtschaftsbeziehungen der "Farinosae." *Ibid.* 3: 169–207. 1962. [Mayacaceae, 180, 191, 192.]
- . Mayacaceae. In: H. MELCHIOR, ed., A. Engler's Syllabus der Pflanzenfamilien. ed. 12. 2: 552. fig. 228, N–S. 1964.
- HARPER, R. M. Botanical explorations in Georgia during the summer of 1901 — II. Noteworthy species. Bull. Torrey Bot. Club 30: 319–342. 1903. [Brief notes on differences between *M. fluviatilis* and *M. Aubletii*, 324, 325.]
- HEGNAUER, R. Chemotaxonomie der Pflanzen. Band 2. Monocotyledoneae. 540 pp. Basel & Stuttgart. 1963. [Mayacaceae, 361, 362.]
- HORN AF RANTZIEN, H. Notes on the Mayacaceae of the Regnellian Herbarium in the Riksmuseum, Stockholm. Sv. Bot. Tidskr. 40: 405–424. 1946. [Monographic study.]
- HOTCHKISS, N. Underwater and floating-leaved plants of the United States and Canada. U. S. Dept. Interior, Fish and Wildlife Service, Bureau of Sport Fisheries and Wildlife, Resource Publ. 44. 124 pp. 1967. [*Mayaca*, 70.]
- HUTCHINSON, J. The families of flowering plants. II. Monocotyledons. xiv + 243 pp. London. 1934. [Mayacaceae, 59–61, *map*.]
- JONES, S. B., JR. Mississippi flora. I. Monocotyledon families with aquatic or wetland species. Gulf Res. Rep. 4: 357–379. 1974. [Mayacaceae, 370, 371, *maps*.]
- KUNTH, C. S. Ueber *Mayaca* Aubl. Abh. Akad. Wiss. Berlin Phys. 1840: 91–94. 1842.
- . Mayaceae Kth. Enumeratio Plantarum 4: 30–33. 1843.
- KUPRIANOVA, L. A. Pollen morphology and phylogeny of the monocotyledons. (In Russian.) Trudy Bot. Inst. Komarova Acad. Nauk. SSSR. 1. Syst. (Acta Inst. Bot. Acad. Sci. URSS. 1. Syst.) 7: 163–262. 1948. [Mayacaceae, 239, 240; descriptions of pollen of *M. fluviatilis* and *M. Kunthii*.]
- LANJOUW, J. Mayacaceae. In: A. PULLE, Fl. Suriname 1(1): 249–251. 1938.
- LINDLEY, J. The vegetable kingdom. lxviii + 908 pp. London. 1846. [Mayacaceae, 189.]
- LOURTEIG, A. Mayacaceae. Not. Syst. Paris 14: 234–248. 1952. [Revision; 4 species recognized.]
- . Distribution géographique des Mayacacées. Compt. Rend. Soc. Biogéogr. 323/325: 31–35. *maps*. 1960.
- . Flora del Uruguay. III. Mayacaceae, Zygophyllaceae, Celastraceae, Lythraceae, Primulaceae. Mus. Nac. Hist. Nat. Montevideo. 38 pp. 1963. [Mayacaceae, 3, 25 (illustration of *M. Sellowiana* and *M. fluviatilis*).]
- . Maiacáceas. In: P. R. REITZ, ed., Fl. Illus. Catarinense. 9 pp. 1965.
- . Sur *Mayaca Sellowiana* (Mayacaceae). Taxon 17: 742, 743. 1968. [Nomenclatural note.]
- . Mayacaceae. In: T. LASSER, ed., Fl. Venezuela 3(1): 1–7. 1971.
- LUDWIG, F. Ueber durch Austrocknen bedingte Keimfähigkeit der Samen einiger Wasserpflanzen. Biol. Centralbl. 6: 299, 300. 1886.
- MACBRIDE, J. F. Mayacaceae. In: Flora of Peru. Publ. Field Mus. Nat. Hist. Bot. 13: 487. 1936. [*M. Endlicheri* Poepp. ex Seubert.]
- MARTIN, A. C. The comparative internal morphology of seeds. Am. Midl. Nat. 36: 513–660. 1946. [Mayacaceae, 533.]
- MEISSNER, C. *Mayaca Vandellii* Schott et Endl. Gartenflora 74: 169, 170. 1925.
- MIRBEL, M. Examen de la division des végétaux en endorhizes et exorhizes.

- Ann. Mus. Hist. Nat. Paris **16**: 419–458. 1810. [Indifferent drawing of seed and embryo of *M. fluviatilis*, pl. 16.]
- MUENSCHER, W. C. Aquatic plants of the United States. x + 374 pp. Ithaca, N. Y. 1944. [Mayacaceae, 189–191, fig. 83.]
- PILGER, R. Mayacaceae. Nat. Pflanzenfam. ed. 2. **15a**: 33–35. 1930.
- POULSEN, V. A. Anatomiske studier over *Mayaca* Aubl. (In Danish; French summary.) Overs. Kongel. Danske Vidensk. Selsk. Forh. Medlemmers Arbejder **1886**(Meddel.): 85–100. pls. 3–7. 1886; **1886**(Résumé): xxi–xxiv. 1887. [*M. lagoensis* Warming and *M. Vandellii* Schott & Endl.]
- RICKETT, H. W. Wildflowers of the United States. Vol. 2. The Southeastern States. Part 1. x + 322 pp. New York. 1966. [*Mayaca*, 64, pl. 19.]
- RUSBY, H. H. Descriptions of new genera and species of plants collected on the Mulford Biological Exploration of the Amazon Valley, 1921–1922. Mem. N. Y. Bot. Gard. **7**: 205–387. 1927. [*M. boliviiana*, sp. nov., 211, 212.]
- SCHLEIDEN, M. J. Grundzüge der Wissenschaftlichen Botanik. ed. 4. xxiv + 710 pp. Leipzig. 1861. [*M. fluviatilis*, 189; reports absence of vessels.]
- SCHNIZLEIN, A. Iconographia familiarum naturalium regni vegetabilis. Vol. 1: Ordines 1–75. Cryptogamae et Monocotyleae. Bonn. 1843–1846. [Mayacaceae, pl. 47*, + 2 unnumbered pages of text.]
- SCULTHORPE, C. D. The biology of aquatic vascular plants. xviii + 610 pp. London. 1967. [See pp. 20, 23, 280, 316, 317, 324, 372, 374.]
- SEUBERT, M. Mayaceae. In: C. F. P. von MARTIUS, Fl. Brasil. **3**(1): [col.] 225–232. pl. 31. 1855.
- SMALL, J. K. Flora of the southeastern United States. xii + 1370 pp. New York. 1903. [Mayacaceae, 231.]
- SMITH, A. C. Mayacaceae. N. Am. Fl. **19**: 1, 2. 1937.
- SOLEREDER, H., & F. J. MEYER. Mayacaceae. In: Systematische Anatomie der Monokotyledonen, Heft **4**: 34–36. Berlin. 1929.
- STANLEY, P. C., & J. A. STEYERMARK. Mayacaceae. In: Flora of Guatemala. Fieldiana Bot. **24**(1): 369, 370. fig. 63. 1958.
- STEBBINS, G. L., & G. S. KHUSH. Variation in the organization of the stomatal complex in the leaf epidermis of monocotyledons and its bearing on their phylogeny. Am. Jour. Bot. **48**: 51–59. 1961. [Mayacaceae, 54, table 2; included among families with two subsidiary cells as the predominant condition.]
- STELLFELD, C. *Mayaca madida* (Vell.) Stellfeld: nova combinação. Tribuna Farmacéut. **35**(1/2): 1, 2. 1967.
- STODOLA, J. Encyclopedia of water plants. 368 pp. T. F. H. Publications, Jersey City, N. J. 1967. [*M. Vandellii*, 264, fig. 147.]
- TIEGHEM, M. P. VAN. Structure de la racine et disposition des radicelles dans les Centrolépidées, Ériocaulées, Joncées, Mayacées et Xyridées. Jour. Bot. Morot **1**: 305–315. 1887. [Mayacaceae, 312, 313.]
- TOMLINSON, P. B. Commelinaceae-Zingiberales. In: C. R. METCALFE, ed., Anatomy of Monocotyledons. Vol. 3. xx + 446 pp. Clarendon Press, Oxford. 1969. [Mayacaceae, 83–91.]
- ULBRICH, E. Ueber die Familie Mayacaceae. Verh. Bot. Ver. Brandenb. **71**: 56, 57. 1929. [Miscellaneous notes.]
- UPHOF, J. C. T. The physiological anatomy of *Mayaca fluviatilis*. Ann. Bot. **38**: 389–393. 1924.
- . Die Blütenbiologie von *Mayaca fluviatilis* Aubl. Ber. Deutsch. Bot. Ges. **51**: 78–85. 1933.

- VESTER, H. Mayacaceae. In: Die Areale und Arealtypen der Angiospermen-Familien. Bot. Archiv 41: 526. fig. 238 (*map*). 1940.*
- WENDT, A. Die Aquarienpflanzen in Wort und Bild. 321 pp. in 16 parts. Alfred Kernen Verlag, Stuttgart. 1952. [Mayacaceae, 253, 254.]
- WOODSON, R. E., JR., & R. W. SCHERY. Mayacaceae. In: Flora of Panama. Ann. Missouri Bot. Gard. 31: 62, 63. 1944.
- ZIEGENSPECK, H. Das Vorkommen von Öl in den Stomata der Monocotyledonen und die Bedeutung des konstitutionalen Vorkommens für die Systematik derselben. Repert. Spec. Nov. 53: 151–173. 1944. [Mayacaceae, 158, 170.]

DEPARTMENT OF BIOLOGICAL SCIENCES
NORTHERN KENTUCKY STATE COLLEGE
HIGHLAND HEIGHTS, KENTUCKY 41076